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Biogeography of species richness gradients: linking adaptive traits, demography and diversification

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ABSTRACT

Here we review how adaptive traits contribute to the emergence and maintenance of species richness gradients through their influence on demographic and diversification processes. We start by reviewing how demographic dynamics change along species richness gradients. Empirical studies show that geographical clines in population parameters and measures of demographic variability are frequent along latitudinal and altitudinal gradients. Demographic variability often increases at the extremes of regional species richness gradients and contributes to shape these gradients. Available studies suggest that adaptive traits significantly influence demographic dynamics, and set the limits of species distributions. Traits related to thermal tolerance, resource use, phenology and dispersal seem to play a significant role. For many traits affecting demography and/or diversification processes, complex mechanistic approaches linking genotype, phenotype and fitness are becoming progressively available. In several taxa, species can be distributed along adaptive trait continuums, i.e. a main axis accounting for the bulk of inter-specific variation in some correlated adaptive traits. It is shown that adaptive trait continuums can provide useful mechanistic frameworks to explain demographic dynamics and diversification in species richness gradients. Finally, we review the existence of sequences of adaptive traits in phylogenies, the interactions of adaptive traits and community context, the clinal variation of traits across geographical gradients, and the role of adaptive traits in determining the history of dispersal and diversification of clades. Overall, we show that the study of demographic and evolutionary mechanisms that shape species richness gradients clearly requires the explicit consideration of adaptive traits. To conclude, future research lines and trends in the field are briefly outlined.

Key words: adaptive trait, adaptive trait continuum, behaviour, clinal variation, demographic variability, diversification, genomics, phylogeny, species richness gradient, systems biology.

CONTENTS

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I. INTRODUCTION

Species richness gradients are among the most widely discussed patterns in ecology (Hutchinson, 1959; Levinton, 1979; MacArthur & Wilson, 1963; MacArthur, Recher & Cody, 1966; Brown, 1981; Rohde, 1992; Ricklefs, 2004, 2006*a*,*b*; Hillebrand, 2004). The relative influence of climate-driven demographic responses and long-term clade diversification dynamics in shaping these gradients is still under debate. The ultimate origin and main driver of species richness gradients is found in the long-term processes of speciation and extinction (long-term diversification dynamics) (Mittelbach *et al.*, 2007). In addition, several studies show that present-day demographical processes significantly covary along species richness gradients, determine the presence or absence of species at the local scale, and thus also contribute to reshape and maintain the observed gradients. It is widely acknowledged that adaptive behaviours and trait evolution can profoundly influence both demographic and diversification dynamics (e.g. Pimentel, 1961; Bolker *et al.*, 2003; Huey, Hertz & Sinervo, 2003; Hairston *et al.*, 2005; Coulson *et al.*, 2006; Reed & Levine, 2005; Sol *et al.*, 2005*a*; Sol, Stirling & Lefebvre, 2005*b*; Fletcher, 2006; Abrams, 2006; Fussman, Loreau & Abrams, 2007; Hendry, Nosil & Rieseberg, 2007; Price, 2008; Carnicer, Abrams & Jordano, 2008*a*). However, a detailed and comprehensive review describing the diverse roles played by adaptive traits on the ecological and evolutionary processes that shape species richness gradients is, to our knowledge, currently lacking. Here we intend to fill this gap by reviewing how adaptive traits can shape species richness gradients through their influence on species' demography and diversification dynamics (see Table 1 for a precise definition of adaptive trait). In the first part of this review we examine how demographic dynamics vary along environmental gradients, and how adaptive traits and demographic mechanisms can actively shape species-richness gradients. In the second part we review the evolutionary mechanisms that mould species richness gradients, emphasizing the influence of adaptive behaviours and adaptive traits on diversification rates and the history of dispersal of clades. Finally, we outline and enumerate some possible future research directions for a trait-based evolutionary ecology of species richness gradients. For practical purposes, the review focuses mainly on terrestrial birds and butterflies. These groups have been intensively studied in the field of species richness gradients and are also in the area of expertise of the authors. Where appropriate, complementary references and examples are provided for plants and other taxonomic groups.

II. ADAPTIVE TRAITS AND DEMOGRAPHIC DYNAMICS IN SPECIES RICHNESS GRADIENTS

(1) Demographic dynamics in species richness gradients

The ultimate origin of species richness gradients clearly relies on the long-term processes of speciation, dispersal and extinction of clades (reviewed in Section III). However, present-day demographic processes are continuously modifying local composition, and determine the presence and absence of species at the local scale, and thus persistently maintain, reorganize and reshape species richness gradients. Here we review how demographic processes influence the shape of species-richness gradients.

Species richness gradients have been empirically associated with geographical gradients of diverse environmental variables such as productivity (Jetz & Rahbek, 2002; Hurlbert & Haskell, 2003; H-Acevedo & Currie, 2003; Hawkins *et al.*, 2003*a*; Hawkins, Porter & Diniz-Filho, 2003*b*; Currie *et al.*, 2004; Pautasso & Gaston, 2005; Evans, James & Gaston, 2006; Mönkönen, Forsman & Bokrna, 2006; Carnicer & Díaz-Delgado, 2008), temperature (Turner, Lennon & Lawrenson, 1988; Currie, 1991; Lennon, Greenwood & Turner, 2000; Jetz & Rahbek, 2002; Forsman & Mönkkönen, 2003; Meehan, Jetz & Brown, 2004; Evans *et al.*, 2006; Carnicer & Díaz-Delgado, 2008), landscape heterogeneity (MacArthur *et al.*, 1966; Lennon *et al.*, 2000; Atauri & de Lucio, 2001; Jetz & Rahbek, 2002; Van Rensburg, Chown & Gaston, 2002; Carnicer & Díaz-Delgado, 2008) or habitat structure (Atauri & de Lucio, 2001; Hurlbert, 2004; Tews *et al.*, 2004; Fuller *et al.*, 2005; Carnicer & Díaz-Delgado, 2008). Recently, Scheiner & Willig (2005) considered the existence of all these diverse associations, and summarized that species richness gradients can be generated by demographic mechanisms if two coupled phenomena occur. First, there is a geographical gradient in one environmental variable (e.g. productivity, habitat availability, temperature, habitat disturbance) or in several spatially correlated environmental variables. Secondly, this environmental gradient causes in turn a geographical gradient in the number of individuals that localities hold (Currie *et al.*, 2004; Scheiner & Willig, 2005; Mönkkönen *et al.*, 2006; Carnicer *et al.*, 2007, 2008*b*; Carnicer & Díaz-Delgado, 2008; Carrascal, Villén-Pérez &

Table 1. Glossary of key concepts and definitions

Glossary	References
Trait: a physical, biochemical, morphological, physiological, phenological or behavioural feature measurable at the individual level, from the cell to whole-organism level.	Violle *et al.* (2007)
Functional trait: a trait that impacts fitness indirectly *via* effects on growth, reproduction and survival (or other related demographic performance variables).	Arnold (1983); Violle *et al.* (2007); Dalziel *et al.* (2009)
Adaptive trait: a functional trait with experimentally quantified effects on organism fitness.	Hodges & Derieg (2009)
Functional/adaptive trait continuum: a significant axis of co-variation between a set of traits observed at the inter-specific level for a taxonomic group, which can be used as a quantitative synthetic measure of life-history variation.	Wright *et al.* (2004); Jeschke & Kokko (2009); Chave *et al.* (2009)
Fitness: a quantitative measure that describes the ability to both survive and reproduce, and is equal to the average contribution to the gene pool of the next generation that is made by an average individual of the specified genotype or phenotype.	Orr (2009)
Trade-off: a linkage between two traits that affects the relative fitness of genotypes and prevents the traits from evolving independently. An increase in fitness due to a change in one trait is opposed by a decrease in fitness due to a concomitant change in a second trait. There are several types of trade-offs like resource allocation trade-offs, resource acquisition trade-offs and specialist-generalist trade-offs.	Angilletta *et al.* (2003)
Demographic/ecological performance variables: a species-specific measure of the rate of biomass maintained, acquired or moved per unit of time, measured at the individual or population level. Examples of demographic performance variables are survival, mortality, fertility, growth and dispersal. Ecological performance can be also assessed by measuring foraging rates, resource acquisition and predator avoidance rates.	Arnold (1983); Violle *et al.* (2007); Dalziel *et al.* (2009)
Demographic dynamics: temporal and spatial variation in the demography (survival, growth, reproduction and dispersal) of individuals and populations.	Kearney & Porter (2009)
Performance curve: a quantitative description of the variation in demographic performance variables along an environmental gradient.	Kearney & Porter (2009)
Habitat and niche variables: species-specific quantitative measures of the abiotic conditions (also termed Grinellian niche) and biotic interactions and resources (also termed Eltonian niche) observed in the localities a species inhabits.	Soberón (2007)
Trait reaction norm: the set of trait phenotypes produced by a single genotype across a range of environmental conditions or environmental gradient.	Stearns (1992)
Dispersal sampling effects: changes in the composition and richness of local communities due to the emigration and immigration of individuals.	Carnicer *et al.* (2007, 2008*b*)
Niche filtering/environmental filtering: the process of local extinction of a individual or a subpopulation due to negative trends in its demographic performance (survival, growth and fertility) driven by interactions between species-specific traits and the environment.	Carnicer *et al.* (2008*b*); Levrija-Trejos *et al.* (2010)

Seoanne, 2011; Table 2). In line with these two conditions, a number of empirical studies state that local environmental conditions frequently co-vary with deterministic parameters of populations (e.g. carrying capacities) along environmental or latitudinal gradients (Sæther *et al.*, 2003, 2008). More generally, more productive areas usually sustain higher total population abundances and an increased number of species (Fig. 1; Mönkkönen *et al.*, 2006; Evans *et al.*, 2006). In turn, areas characterized by higher densities usually display greater recruitment *per capita* and per unit of land area (Bock & Jones, 2004). All this empirical evidence suggests the existence of an active causal link between regional demographic dynamics and the shape of species richness gradients.

Moreover, environmental gradients can also influence the variability of local population dynamics (Thomas, Moss & Pollard, 1994; Sæther *et al.*, 2008; Oliver *et al.*, 2010). Localities with reduced community sizes (lower habitat quality and population abundances) experience increased turnover rates and greater extinction rates and increased effects of demographic stochasticity. All these processes contribute to shape species richness gradients (Fig. 1; Boulinier *et al.*, 1998; Krauss, Steffan-Dewenter & Tscharntke, 2003; Evans, Greenwood & Gaston, 2005*a*; Evans, Warren & Gaston, 2005*b*; Carnicer *et al.*, 2007, 2008*b*; Sæther *et al.*, 2011). Small populations differ markedly in their local dynamics, being affected to a greater extent by Allee effects, inbreeding effects, demographic variability, extinction events and emigration (Kuussaari, Nieminen & Hanski, 1996; Kuussaari *et al.*, 1998; Saccheri *et al.*, 1998; Stephens & Sutherland, 1999; Greene & Stamps, 2001; Orrock & Fletcher, 2005; Melbourne & Hastings, 2008; Sæther *et al.*, 2011).

Environmental gradients and geographic variation in habitat quality (*sensu* Johnson, 2007) may in turn influence

Table 2. A non-exhautive list of some demographic mechanisms that can potentially shape species richness gradients

Scale	Ecological Processes		Theory
Regional	Regional dispersal dynamics	Sampling effects by dispersal processes	Localities with higher habitat quality usually sustain increased numbers of individuals. Sampling effects produced by species-specific dispersal processes from source areas can shape species richness gradients.
		Colonization, dispersal and habitat-selection behaviour	Colonization and dispersal dynamics are mediated by species-specific habitat selection and dispersal behaviours (adaptive behavioural traits).
		Niche/habitat filtering	Local conditions and resources will interact with the adaptive traits of species, influence their local demographic and dispersal rates and filter the species that are incorporated from regional pools or source regions.
Local	Demographic dynamics	Demographic effects of environmental conditions	Effects of environmental variables on deterministic components of population dynamics (e.g. carrying capacity, survival) originate geographical gradients in abundance and shape species richness gradients.
		Abundance-extinction dynamics (demographic and environmental stochasticity)	Increased negative effects of demographic variability in localities with reduced community size and small population sizes increase extinction risk and shape species richness gradients (e.g. Fig. 2). Extinction risk is usually higher in species with specialized adaptive traits and lifestyles (e.g. Koh *et al.*, 2004; Kotiaho *et al.*, 2005). Long-term demographic dynamics that sustain species-richness gradients are influenced by species-specific adaptive traits (e.g. Fig. 3B).
		Local interactions	Interactions between species, resources and environmental conditions limit/enhance local population persistence, define local composition and limit species' ranges.

regional dispersal dynamics (Paradis *et al.*, 1998; Parejo *et al.*, 2007; Studds, Kyser & Marra, 2008; Baguette, Clobert & Schtickzelle, 2011; Alexander *et al.*, 2011). Localities with smaller community sizes (i.e. lower habitat quality and reduced total number of individuals) are expected to hold a reduced number of species by dispersal-limited sampling from more productive source areas in theoretical models (Hubbell, 2001; Vellend, 2005). These trends are supported by empirical studies (Coleman *et al.*, 1982; Carnicer *et al.*, 2007, 2008*b*; Honkanen *et al.*, 2011; Alexander *et al.*, 2011; Kraft *et al.*, 2011). Remarkably, these dispersal-limited sampling effects are also significantly influenced by the number of species available in the different biogeographic pools that contribute to a specific locality (e.g. Pärtel, 2002; Pärtel, Laanisto & Zobel, 2007; Kozak & Wiens, 2010; Grace, Harrison & Damschen, 2011). Widespread and abundant generalists are more prone to successfully colonizing localities with low community sizes whereas less-abundant species (at the regional level) are more frequently absent (Fig. 2; Carnicer *et al.*, 2008*b*; Alexander *et al.*, 2011). The coexistence of habitat-generalist and -specialist strategies can produce spatially nested patterns in the distributions of the species that finally shape regional gradients (Fig. 2). Several studies indicate that the temporal demographic dynamics of widespread habitat generalists and rare habitat specialists are qualitatively different. Demographic dynamics of populations of widespread and abundant habitat generalists tend to co-vary synchronously at larger scales, tracking large-scale environmental variation, whereas different small populations of rare species and habitat specialists often vary asynchronously, are much more affected by demographic stochasticity and are less synchronized with environmental variation (Hanski & Woiwod, 1993; Sutcliffe, Thomas & Moss, 1996; Sæther *et al.*, 2011).

(2) Adaptive traits and demographic dynamics

Population dynamics can be strongly influenced by adaptive behaviours and traits (Koh, Sodhi & Brook, 2004; Kotiaho *et al.*, 2005; Helm, Piersma & van der Jeugd, 2006; Hanski & Saccheri, 2006; Poorter *et al.*, 2008; Hoffmann, 2010; Hanski & Mononen, 2011). Colonization rates, extinction events and demographic rates are influenced by species adaptations in habitat selection behaviour, dispersal behaviour, niche breadth and life-history traits (Brändle *et al.*, 2002; Wiens & Donoghue, 2004; Sol *et al.*, 2005*a*; Sol, Stirling & Lefebvre, 2005*b*; Carnicer *et al.*, 2008*b*; Sæther *et al.*, 2011, Hanski & Mononen, 2011). Arguably, a limited set of species-specific adaptive traits should regulate the demographic dynamics that limit species distributions and eventually shape species richness gradients. Available studies suggest that in many cases a significant role is played by traits related to thermal or aridity tolerance, host-plant or resource use, phenology and dispersal (e.g. Kellermann *et al.*, 2009; Chuine, 2010; Stefanescu, Carnicer & Peñuelas, 2011*a*). For instance, experimental studies indicate that low genetic variation on thermal adaptive traits can reduce population growth and determine higher extinction risk in localities near the

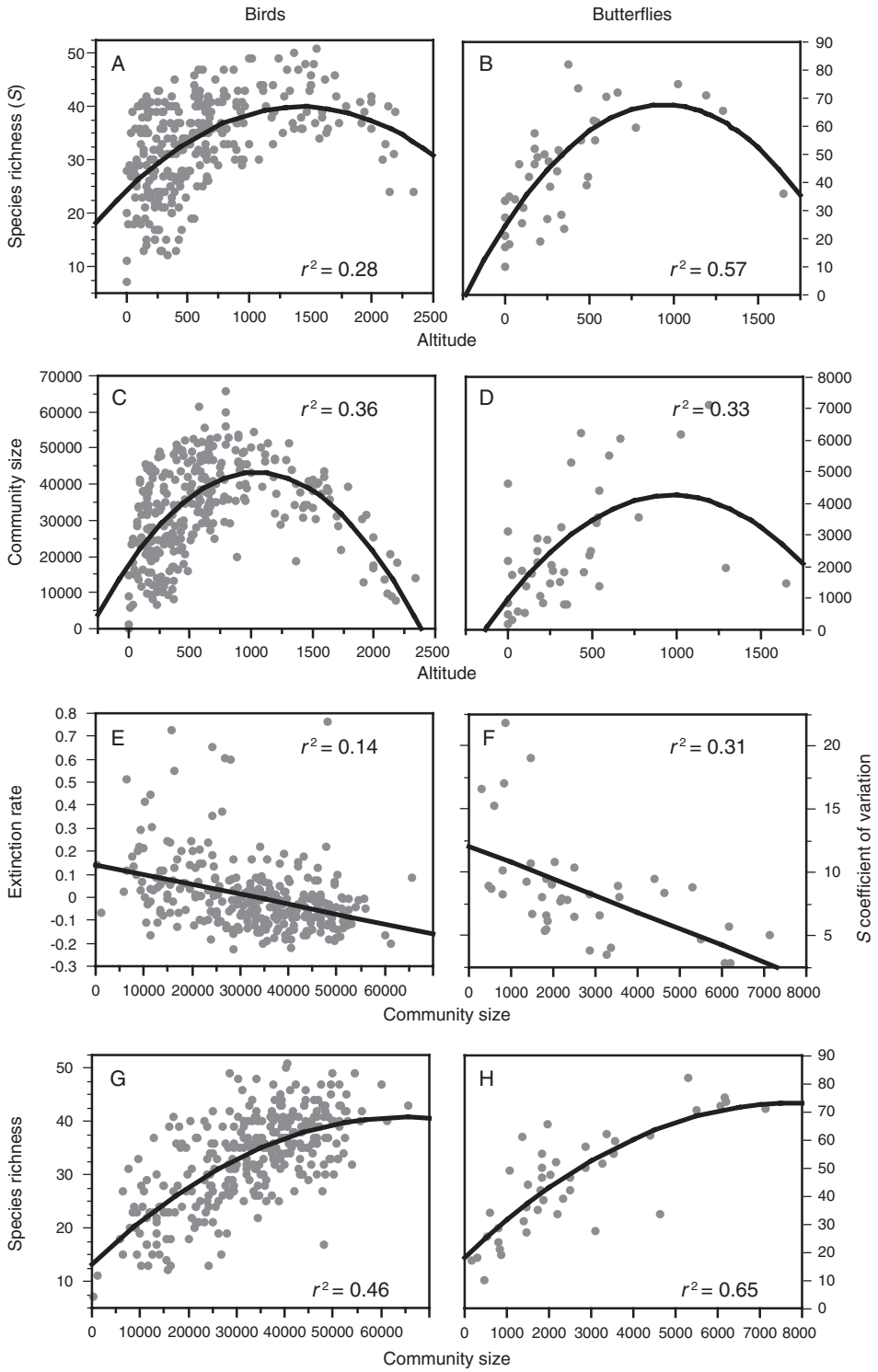

Fig. 1. Parallel altitudinal species-richness gradients of butterflies and forest birds in Catalonia (Spain). (A, B) Altitudinal variation of bird and butterfly species richness. (C, D) Altitudinal variation of community size (total number of individuals of birds and butterflies, respectively). (E, F) Observed abundance-extinction dynamics for birds and butterflies: (E) reduction in the proportion of forest bird species that became locally extinct with increased community size; (F) observed decrease in the temporal coefficient of variation of butterfly species richness with increased community size. Bird extinction numbers were calculated comparing two separate field survey periods: 1980–83 and 1999–2002 (Carnicer *et al.*, 2007). The temporal coefficient of variation of butterfly species richness was calculated from annual surveys for the 1988–2007 time period. (G, H) Observed relationships between species richness and community size for birds and butterflies. All fitted models were significant with $P < 0.0001$.

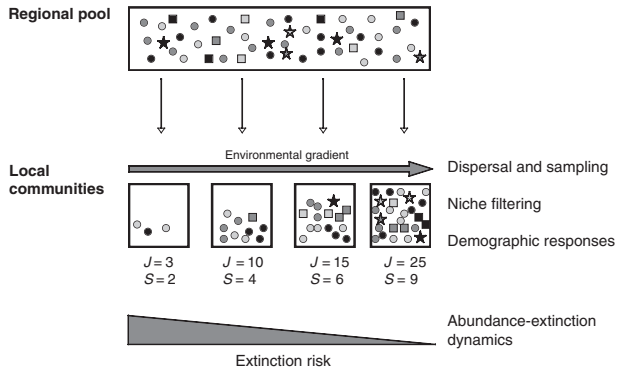

Fig. 2. An illustrative scheme explaining how regional dispersal dynamics (i.e. local sampling by dispersal processes), niche-filtering and local population dynamics can shape species-richness gradients at the regional scale. Stars, circles and squares represent individuals of different species. Each species is represented by a unique combination of shape and shading. The environmental gradient originates a gradient in the total number of individuals that localities hold (community size or ***J***). Localities with greater community sizes (***J***) may sustain increased species richness (*S*) by local positive demographic responses and by dispersal sampling effects from other source areas. Widespread and abundant species (circles) are preferentially included in localities with low community sizes (low-quality sites). Squares represent species with intermediate life histories between specialist and generalist lifestyles. Niche filtering occurs in species with more selective habitat preferences (stars). Note that habitat specialists (stars) colonize only specific environments (high-***J*** localities) whereas generalists (circles) occupy different types of localities (high- and low-***J*** localities) leading to a geographically nested structure. Localities with extreme environmental conditions sustain small population sizes. This increases the extinction risk of populations and may cause an additional decrease in local species richness (abundance-extinction dynamics).

thermal tolerance limit of the species (Willi & Hoffmann, 2009; Hoffmann, 2010). Similarly, low heritable variation and low evolvability in thermal adaptive traits is associated with the limits of the geographical distributions of insects (Kellermann *et al.*, 2009; Hoffmann, 2010).

Phenological traits also influence reproductive rates and survival at the limits of species distributions (Chuine, 2010; Visser *et al.*, 2010). Phenological traits are usually integrated in complex schedules, i.e. seasonally ordered annual sequences of behaviours that are genetically programmed (Helm *et al.*, 2006; Salewski & Bruderer 2007; Wikelski *et al.*, 2008; Liedvogel *et al.*, 2009; Visser *et al.*, 2010) and plastically adjusted by some environmental and social cues perceived by species (e.g. Doligez *et al.*, 2003; Helm *et al.*, 2006; Fletcher, 2007; Forsman *et al.*, 2008; Studds *et al.*, 2008; Visser *et al.*, 2010). For instance, in birds, behavioural schedules can include autumn and spring migration, breeding and territorial behaviour, natal and adult dispersal, moult, and wintering flocking. Interestingly, available studies suggest important effects of bird behavioural schedules in the seasonal and spatial variance of patterns of species richness gradients (e.g. effects of migration in bird species richness gradients; Hurlbert & Haskell, 2003; Carnicer & Díaz-Delgado, 2008). Similarly, important effects of insect diapause and phenology are detected on latitudinal and altitudinal distributions (e.g. Schmidt & Paaby, 2008).

Diverse adaptive traits and behaviours can strongly determine dispersal capacities and thus may determine sampling effects and the shape of regional species richness gradients (Table 2). Some examples of these adaptive behaviours are conspecific and heterospecific attraction and repulsion, public information gathering, and species-specific behavioural barriers to dispersal. Moreover, many species have evolutionarily developed condition-dependent dispersal strategies (Bowler & Benton, 2005, Clobert *et al.*, 2009), and plastically respond to the spatial and temporal variation of the costs of dispersal. For example, empirical studies in a number of bird species assert that breeding dispersal and settlement can be behaviourally driven by public information gathered by postfledging juveniles and adults to assess the suitability of future breeding sites (Doligez, Danchin & Clobert, 2002; Doligez *et al.*, 2003; Danchin *et al.*, 2004; Dall *et al.*, 2005; Parejo *et al.*, 2007). In making settlement decisions, birds evaluate diverse cues like local food availability (Tellería, Ramírez & Pérez-Tris, 2008; Forsman *et al.*, 2008), competitor density (Forsman *et al.*, 2008) and local predation risk (Harris & Reed, 2002; Thomson *et al.*, 2006). Condition-dependent dispersal responses are also observed in butterflies, insects and other taxonomic groups (Clobert *et al.*, 2009; Baguette *et al.*, 2011).

On the other hand dispersal is restricted by species-specific behavioural barriers (Reed, 1999; Ries & Debinski, 2001; Harris & Reed, 2002; Koh *et al.*, 2004; Kotiaho *et al.*, 2005; Reed & Levine, 2005; Clobert *et al.*, 2009). Habitat fragmentation, gaps and ecotones can be more common at the extremes of regional species richness gradients (e.g. Carnicer *et al.*, 2007) and are frequently perceived as barriers to movement by some species but not for others (Desrochers & Hannon, 1997; Ries & Debinski, 2001) because species are characterized by specific threshold distances to movement across certain habitat types (Harris & Reed, 2002; Moore *et al.*, 2008). Generally, behavioural barriers to dispersal vary among functional groups, being usually greater in habitat specialists and resident species (Haddad & Baum, 1999; Desrochers & Hannon, 1997; Ries & Debinski, 2001; Harris & Reed, 2002; Kotiaho *et al.*, 2005). Finally, phenotypic plasticity and heritable variation on dispersal capacity is frequent at both the intra- and inter-specific level. Indeed, both aspects have been extensively documented, influencing population dynamics and range-expansion processes (Thomas *et al.*, 2001; Ovaskainen *et al.*, 2008; Niitepõld *et al.*, 2009; Clobert *et al.*, 2009; Stevens, Turlure & Baguette, 2010).

Overall, a number of adaptive behaviours and traits can cause spatial aggregative responses, promote dispersal processes and determine dispersal dynamics along regional species richness gradients; but are rarely considered in the macroecological analyses of regional species richness

gradients. Moreover, theoretical studies indicate that population dynamics that shape species richness gradients at local or regional scales may be substantially influenced by these behavioural adaptive traits. For instance, behaviours such as conspecific and heterospecific attraction displayed during breeding and habitat selection (Stamps, 1988, 1991; Mönkkönen, Helle & Soppela, 1990; Fletcher, 2007) can profoundly influence metapopulation source-sink dynamics (e.g. Reed, 1999; Sæther, Engen & Lande, 1999; Greene & Stamps, 2001; Greene, 2003; Reed & Levine, 2005; Fletcher, 2006, 2007). Generally, theoretical models that incorporate conspecific aggregative responses produce an increase in extinction rates and reductions in colonization rates, leading to metapopulations with reduced viability. Individuals that display conspecific attraction behaviour tend to immigrate into already occupied patches, decreasing the colonization rate of empty patches. On the other hand, models with conspecific repulsion confer higher viability to modeled metapopulations (Bowler & Benton, 2005). Similarly, Reed & Levine (2005) modelled metapopulation persistence based on diverse species-specific behaviours that influence colonization, extinction and rescue effects. In sum, available empirical and theoretical evidence suggests that dispersal along species-richness gradients is usually a non-random process in which species-specific adaptive traits, behavioural responses and condition-dependent responses play a major role.

Local population dynamics, regional dispersal dynamics, evolutionary dynamics of adaptive traits and diversification processes are not independent processes (Johnson & Stinchcombe, 2007; Fussman *et al.*, 2007). For instance, behavioural and morphological traits affecting dispersal capacity (Böhning-Gaese, González-Guzmán & Brown, 1998; Böhning-Gaese *et al.*, 2006) and niche breadth (Brändle *et al.*, 2002) might shape species richness gradients through both demographic and evolutionary dynamics. Indeed, the effect of such adaptive traits is twofold: demographically, they determine differences in species colonizing, extinction and population growth rates that actively shape present-day gradients (Table 2; Wiens & Donoghue, 2004; Wiens & Graham, 2005; Hanski & Saccheri, 2006; Kotiaho *et al.*, 2005); evolutionarily, they may determine gene flow and long-term diversification dynamics (Phillimore *et al.*, 2006; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010). For instance, existing empirical evidence states that clades with increased dispersal abilities are more able to both expand their ranges and diversify (Böhning-Gaese *et al.*, 2006; Phillimore *et al.*, 2006, 2007; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010; but see Belliure *et al.*, 2000).

III. ADAPTIVE TRAITS AND DIVERSIFICATION DYNAMICS IN SPECIES RICHNESS GRADIENTS

Species richness gradients can be generated by evolutionary mechanisms *via* geographical gradients in different variables: speciation rates (Cardillo, 1999; Fjeldsa & Rahbek, 2006; Weir, 2006; Ricklefs, 2006*b*; Weir & Schluter, 2007), lineage extinction rates (Hawkins *et al.*, 2007; Wiens, 2007), geographical area suitable for speciation (Rosenzweig, 1995; Pärtel *et al.*, 2007; Fine & Ree, 2006; Vamosi & Vamosi, 2010; Zobel *et al.*, 2011), time to diversify (Stephens & Wiens, 2003; Fine & Ree, 2006; Benton & Emerson, 2007; Hawkins *et al.*, 2007; Wiens, Pyron & Moen, 2011) and historical dispersal clines (Hawkins *et al.*, 2007; Roy & Goldberg, 2007; Wiens, 2007). All these processes may be influenced by the adaptive traits of species and their lifestyles (Table 3). For instance, adaptive traits can influence speciation and extinction rates (Kotiaho *et al.*, 2005; Rabosky, 2009; Vamosi & Vamosi, 2010) and influence historical dispersal clines (Van Bocxlaer *et al.*, 2010).

A latitudinal gradient of increasing diversification rates with decreasing latitude has been described empirically in birds, butterflies, plants and other groups (Cardillo, 1999; Ricklefs, 2006*b*; Wright, Keeling & Gillman, 2006; Weir & Schluter, 2007; Wiens, 2007). However, the relative importance of lineage extinction rates, speciation rates, area, time and dispersal movements in generating species richness gradients is not well understood yet (Weir, 2006; Hawkins *et al.*, 2007; Wiens, 2007; Weir & Schluter, 2007). Available evidence suggests that all these processes are effectively contributing to the generation of the latitudinal gradients of species richness (Goldberg *et al.*, 2005; Fjeldsa & Rahbek, 2006; Hawkins *et al.*, 2007; Wiens, 2007; Roy & Goldberg, 2007; Van Bocxlaer *et al.*, 2010) and therefore the debate is centred in contrasting and evaluating the relative importance of all the processes listed in Table 3. Below we elaborate on those research areas that are needed to achieve a more precise view of the role of adaptive traits on the evolutionary processes that affect species richness gradients.

(1) Genetic basis of adaptive traits—mechanistic approaches linking genotype, phenotype and fitness

The application of genomics and high-throughput techniques greatly facilitates the identification of the genes underlying ecologically important traits (e.g. Vasemägi & Primmer, 2005; Hoekstra *et al.*, 2006; Jensen, Wong & Aquadro, 2007; Naish & Hard, 2008; Ellegren & Sheldon, 2008; Pavlidis, Hutter & Stephan, 2008; Stinchcombe & Hoekstra, 2008; Slate *et al.*, 2009), and the identification of genes and traits specifically involved in speciation and reproductive isolation (Schluter, 2009; Wolf, Lindsell & Backström, 2010; Presgraves, 2010; Backström *et al.*, 2010; Rieseberg & Blackman, 2010; Nosil & Schluter, 2011; Rice *et al.*, 2011). Moreover, in a quite reduced number of well-described adaptive traits, mechanistic approaches linking genotype, phenotype and fitness effects can be implemented (reviewed in Dalziel, Rogers & Schulte, 2009). These approaches provide descriptions of adaptive traits at several hierarchical levels (genetic variation, protein function, biochemical networks, neuro-molecular and hormonal function, whole-organism behavioural and physiological performance, and fitness differences) (Dalziel *et al.*, 2009; Dillon *et al.*, 2009; Palsson, 2009). Notably, these complex approaches are becoming progressively available for some adaptive traits that

Table 3. A non-exhaustive list of some evolutionary mechanisms that can potentially influence species richness gradients

Scale	Evolutionary processes	Theory
Regional	Geographic mosaics of selection and speciation rates	Geographic differences in selection can promote differences in speciation rates between areas and potentially originate clines in species richness. Rates of speciation can be increased or reduced by clade-specific adaptive traits (Sargent, 2004) and by the interaction of adaptive traits and the environment (De Queiroz, 2002).
	Geographic mosaics in extinction rates	Extinction risk can vary geographically. Increased lineage extinction rates due to regional climate and vegetation shifts can create gradients in species richness. Rates of extinction are significantly influenced by the adaptive traits of species, being usually higher in specialized lifestyles (e.g. Kotiaho *et al.*, 2005).
	Diversification area	Larger habitat areas may allow for increased total diversification rates and higher species richness.
	Diversification time	Larger diversification time in the tropics and other areas may have produced increased cumulative diversification rates.
	Historical dispersal clines	Historical dispersal clines from centres of diversification yield to species richness clines with maximum values usually near the origin point. Adaptive traits associated with dispersal and trophic generalism explain differences in historical dispersal clines of clades (Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010).
	Range expansion, isolation and allopatric diversification	Topographic barriers can facilitate the emergence of species-richness gradients if populations of formerly widespread species become isolated by mountain chains or other geographical barriers and diversify by independent evolutionary paths and local adaptation.
	Specialist/generalist transition dynamics	Diversification dynamics often oscillate between range expansion phases (often associated with the geographical expansion of clades characterized by high-dispersal and generalist adaptive traits) and specialization phases (often associated with the emergence of more specialized adaptive traits and local specialization) (Janz & Nylin, 2008; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010). A latitudinal increase of the proportion of specialists has been detected in some groups (Scriber, 1973; Dyer *et al.*, 2007). Specialist-generalist life history variation can be synthetically described by adaptive trait continuums in some clades (e.g. Fig 3).
Local	Community context	Geographical gradients of local interactions, such as competition, parasitism, facilitation, predation or mutualism, can promote divergent or convergent selection on adaptive traits, influence extinction and diversification rates and shape species-richness gradients.
	Uneven spatio-temporal distribution of resources	Uneven spatiotemporal distribution of resources promotes the emergence of different adaptive foraging behavioural strategies and phenologies, the emergence of migratory behaviours, drives diversification processes and contributes to shape species-richness gradients.
	Phenotypically plastic responses	Phenotypically plastic responses drive local selection pressures on adaptive traits and influence diversification processes.

determine species' ranges and the shape of species-richness gradients, like thermal preference and aridity tolerance (Dillon *et al.*, 2009; Kellermann *et al.*, 2009; Hoffmann, 2010; Paaby *et al.*, 2010), phenological traits (Flowers *et al.*, 2009; Chuine, 2010; Visser *et al.*, 2010) and dispersal capacity (Dalziel *et al.*, 2009; Wheat *et al.*, 2011). Similarly, integrative descriptions of suites of traits involved in the emergence of reproductive isolation and speciation are becoming available for plants, birds, butterflies, and other groups (Bradshaw & Schemske, 2003; Shapiro *et al.*, 2004; Kronforst *et al.*, 2006; Abzhanov *et al.*, 2006; Seehausen *et al.*, 2008; Hodges & Derieg, 2009; Chamberlain *et al.*, 2009; Bomblies & Weigel, 2010; Wolf *et al.*, 2010; Baxter *et al.*, 2010; Hohenlohe *et al.*, 2010; McBride & Singer, 2010; Sætre & Sæther, 2010). Interestingly, these integrative mechanistic approaches can be successfully applied to the study of the evolutionary processes in species richness gradients (Table 3), for example specifically allowing the study of speciation processes along environmental gradients. For instance, Seehausen *et al.* (2008) studied the species of cichlid fishes distributed along several replicated environmental gradients in the islands of Lake Victoria. After several years of combined field, experimental and molecular studies, they were able to quantify precisely a suite of traits at several hierarchical levels of organization (ecological, behavioural and molecular traits) that experienced divergent evolution and were significantly associated with reproductive isolation and sympatric speciation in these gradients. Notably, differences in the slope of the environmental gradients in Lake Victoria explained the observed variation in the progress and completeness of speciation: speciation occurred on all but the steepest gradients (Seehausen *et al.*, 2008). Remarkably, these empirical trends fully matched recent theoretical models of clinal speciation predicting the emergence of speciation at environmental gradients of intermediate slopes (Doebeli & Dieckmann, 2003; Heinz, Mazzucco & Dieckmann, 2009).

(2) Sequences of adaptive traits along phylogenies

Molecular phylogenetic studies frequently report specific traits (often called key innovations) significantly associated

with the emergence of adaptive radiations and speciation events (Heard & Hauser, 1995; Webb *et al.*, 2002; Ree, 2005; Vitt & Pianka, 2005; Paradis, 2005; Donoghue, 2005; Ackerly, Schwilk & Webb, 2006; Wheat *et al.*, 2007; Seehausen *et al.*, 2008; Menken, Boomsma & Van Nieukerken, 2009; Hodges & Derieg, 2009; Wolf *et al.*, 2010; Glor, 2010). For instance, Streelman & Danley (2003) highlighted that vertebrate radiations usually follow similar trajectories, diverging first in characters associated with habitat selection, then in foraging morphology and finally in communication or sexually related traits. The general model pointed out by Streelman & Danley (2003) has empirical support in some bird clades, as morphological shifts in bird characters associated with habitat use can usually be traced to the most internal nodes of the phylogeny in a number of clades (Desrochers & Diamond, 1986; Richman, 1996; Price, 1998; Ricklefs, 2007). Subsequent diversifications in some bird phylogenies are then based on traits associated with foraging behaviour and resource-tracking movements, such as beak shape, body size and wing length (Price, 1998; Remsen, 2003; Burns, Hackett & Klein, 2003; Ricklefs, 2007). However, this general scheme of diversification is likely to apply only in some cases and should be observed with caution for several reasons. First, some studies document the possibility of rapid evolution in morphological traits associated with habitat and resource use, suggesting again that trait sequences might easily differ among clades (Böhning-Gaese & Oberrath, 1999; Smith *et al.*, 1997; Böhning-Gaese, Schuda & Helbig, 2003). Second, trait sequences implied in diversification possibly are much more complex than the evolutionary hypothetical sequences outlined until now (e.g. Price, 1998) and might be site specific. For instance, apart from foraging and habitat-use traits, a considerable number of additional traits have been found to be involved in bird speciation processes (Table 4). Third, a variety of different processes not associated with species traits can influence speciation rates in a non-sequential manner.

In Lepidoptera, Menken *et al.* (2009) recently described a phylogenetic sequence of key adaptive traits. Initial diversifications are related to a trophic switch from litter feeding to leaf herbivory, and with the emergence of internal larval feeding (e.g. mining, galling, boring) and monophagous diets. Later, derived adaptive traits related to the evolution of exposed feeding (e.g. larval locomotory morphology, dessication tolerance, larval size, digestive metabolism) and larval generalist feeding progressively increase in frequency along the phylogeny, albeit with frequent reversals and specialist-generalist transitions (sensu Janz & Nylin, 2008).

In the case of plants, Donoghue (2005) has reviewed which sequences of key adaptive traits occurred at the initial splits of plant phylogenies; and Ackerly *et al.* (2006) highlighted that small-scale components of the niche that differ among co-occurring species (such as microhabitat use) usually diverge early in the phylogeny during adaptive radiations in plants. At more derived levels of plant phylogenies, higher speciation rates are often positively associated with biotic pollination and floral asymmetry (Sargent, 2004; Vamosi & Vamosi, 2010), herbaceous life form (Ricklefs & Renner, 1994; Vamosi & Vamosi, 2010), shorter generation times (Smith & Donoghue, 2008) and self-incompatibility (Igic, Lande & Kohn, 2008, Goldberg *et al.*, 2010), and negatively associated with dioecy (Heilbuth, 2000).

Overall, a considerable number of traits have been associated with diversification processes in different taxonomic groups and in some clades can be ordered sequentially providing some initial evolutionary hypotheses. Of course, much more detailed phylogenetic analyses are yet required to derive a general quantitative perspective of the sequential order and importance of traits implied in each specific group and geographic site (Ree, 2005; Paradis, 2005; Phillimore *et al.*, 2007; Menken *et al.*, 2009, Kozak & Wiens, 2011), and the genetic and developmental paths involved in the regulation of these traits (Wu *et al.*, 2004; Abzhanov *et al.*, 2004; Fitzpatrick *et al.*, 2005; Donoghue, 2005). Nevertheless, some pioneering studies show the potential of multi-trait comparative phylogenetic studies in explaining worldwide radiations and diversity patterns for a determinate taxonomic group. For instance, van Boxclaer *et al.* (2010) used a multiple-trait comparative phylogenetic analysis to study the evolution of highly dispersive and low-dispersive toad species during the last 55 million years. This study covered 228 taxa (43% of extant bufonid species diversity) distributed worldwide. Their analysis allowed the identification of an optimal range-expansion phenotype, based on a suite of traits (body size, presence of inguinal fat bodies, aquatic and opportunistic oviposition site, large clutch size and exotrophous larvae) and habitat-use variables (semi-terrestrial adult habitat). Interestingly, van Boxclaer *et al.* (2010) were able to: (1) provide a worldwide reconstruction of the more plausible history of phenotype evolution for the bufonid clade, (2) link changes in multi-trait phenotype evolution with the temporal dynamics of diversification rates during the last 55 million years, (3) significantly associate the observed increases in estimates of net diversification rates during the Eocene and Oligocene with the emergence of a highly dispersive multi-trait phenotype, and (4) explain the worldwide geographic expansion of the bufonid clade. Overall, this pioneering study provided a worldwide synthetic view of how trait evolution moulded the geographic diversification of toads during the last 55 million years in time and space.

(3) The role of adaptive traits in the history of biogeographical movements of clades

The consideration of historical diversification centres and clade historical dispersal clines is essential for the understanding of the historical generation of global and regional species richness gradients (e.g. Ericson, Irestedt & Johansson, 2003; Hawkins *et al.*, 2007; Roy & Goldberg, 2007). Episodes of biogeographic movement and/or isolation are in some cases associated with clear shifts in the diversification rates of clades (Moore & Donoghue, 2007). For example, empirical evidence supports that colonization of mountain chains

Table 4. Some adaptive traits associated with speciation in birds

Habitat selection traits	Morphological traits associated with habitat-use behaviour differ among some bird clades during the initial splits of the phylogeny (Desrochers & Diamond, 1986; Price, 1998; Ricklefs, 2007).
Size and foraging traits	After this initial divergence in habitat-use-related traits, subsequent diversifications are usually based on body size and/or traits associated with foraging behaviour (Price, 1998).
Dispersal traits	Traits that enhance dispersal, colonization and migration can have long-term effects on the diversification dynamics of clades (Böhning-Gaese *et al.*, 1998; Irwin & Irwin, 2005; Phillimore *et al.*, 2007; Moyle *et al.*, 2009). For instance, the number of bird subspecies covaries with migratory habits and geographical range size (Belliure *et al.*, 2000; Phillimore *et al.*, 2007). Traits associated with enhanced dispersal and migratory ability possibly evolved from local-area feeding strategies such as seasonal resource tracking and altitudinal movements (Levey & Stiles, 1992; Mettke-Hofmann & Gwinner, 2004; Boyle & Conway, 2007; Carnicer *et al.*, 2008*a*). Subsequently, such behaviours could potentially have facilitated colonization, range expansion and allopatric diversification processes in a number of bird clades (Irwin & Irwin, 2005; Phillimore *et al.*, 2006; Böhning-Gaese *et al.*, 2006; Moyle *et al.*, 2009).
Mate-choice traits	Geographical divergence in characters involved in mate choice, such as song, plumage, and behavioural displays are likely to play important roles in avian speciation (Møller & Cuervo, 1998; Edwards *et al.*, 2005), albeit some authors have suggested that the role is secondary when compared with other factors such as dispersal, range size or feeding generalization (Price, 1998; Phillimore *et al.*, 2006). Gradual divergence of song in allopatric populations may result in reproductive isolation upon secondary contact and speciation (Grant & Grant, 1997; Irwin, 2000; Irwin *et al.*, 2001*a*,*b*, 2005; Edwards *et al.*, 2005; Toews & Irwin, 2008). Songs have been found to diverge as a result of habitat-dependent selection or indirectly as a consequence of morphological adaptations (Podos, 2001; Slabbekoorn & Smith, 2002*a*, *b*; Patten *et al.*, 2004; Seddon, 2005). Other studies, however, support the importance of stochastic evolution of songs in the evolution of new species (Miyasato & Baker, 1999; Irwin *et al.*, 2008). In some specific clades, song can act as a key character determining diversification dynamics. Indeed, song learning and sexual imprinting explain the sympatric diversification of brood parasitic indigobirds (Sorenson *et al.*, 2003). Similarly, sexually selected traits predict patterns of species richness in antbirds (Seddon *et al.*, 2008).
Cognitive traits	A larger relative brain size has been found to enhance bird cognitive skills thus promoting feeding generalization and enabling the use of new resources (Lefevbre *et al.*, 1997). This increase in phenotypic plasticity in big-brained birds can increase diversification rates by two causal paths. First, increased relative brain size has been found to allow birds to shift to new adaptive zones thus promoting morphological diversification (Wyles *et al.*, 1983; Sol *et al.*, 2005*b*; Sol & Price, 2008). Second, big-brained individuals might more easily spread to new locations increasing opportunities for allopatric speciation and reducing extinction risk (Sol *et al.*, 2002, 2005*a*, *b*; Sol & Price, 2008).

favoured isolation and strongly increased diversification rates in birds, butterflies, plants and other taxa (Weir, 2006; Fjeldsa & Rahbek, 2006; Hughes & Eastwood, 2006; Johansson *et al.*, 2007; Moore & Donoghue, 2007; Price, 2008). Jablonski, Roy & Valentine (2006) proposed a general verbal model of global diversification (the "Out of the Tropics" model) in which the bulk of the clades preferentially originate in the tropics and only some of them expand towards the poles leading to secondary diversification processes there. This general scheme matches the observed phylogenetic trends in bird and butterfly species richness-gradients at a global scale (Hawkins *et al.*, 2007; Hawkins, 2010), although exceptions exist and are to be expected in a number of clades (Ericson *et al.*, 2003; Wiens, 2007). Similarly, in the Passerida clade a longitudinal gradient in species richness from their centres of diversification in South East Asia has been described, presumably reflecting both an historical dispersal cline and a time-for-speciation effect (Hawkins *et al.*, 2007). Elsewhere, Richman (1996) showed that *Phylloscopus* warblers spread by multiple invasions from mainland Asia, with only limited subsequent speciation and little associated morphological diversification. Notably, some pioneering studies are starting to analyze the role of adaptive traits in these historical processes of range expansion and diversification (Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010). These studies suggest that the acquisition of traits associated with a high dispersal capacity and a generalist trophic position play a major role on range expansion phases. Range expansion phases are in some cases followed by subsequent phases of local specialization and speciation, in which adaptive traits associated with specialist life histories evolve (e.g. Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010). Similarly, in some ectotherm clades like salamanders, the acquisition of higher metabolic rates is associated with increased dispersal capacity, broader thermal tolerance and the expansion of distributional ranges (Bernardo *et al.*, 2007). Genetic links between dispersal capacity, metabolic rate, population growth rate, and range distribution of insects have also been documented (reviewed in Dalziel *et al.*, 2009). Together, this body of empirical evidence indicates that adaptive traits mediate specialist-generalist transitions, promote range expansion phases and influence the dynamics of diversification during the dispersal of clades (Janz & Nylin, 2008; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010; Vamosi & Vamosi, 2010).

(4) Clinal variation of adaptive traits

The study of clinal variation of adaptive traits along parallel environmental gradients provides an ideal scenario to examine how trait-environment interactions may limit species' distributions, and thus contribute to shape species-richness gradients (Schmidt *et al.*, 2008*a*; Kolaczkowski *et al.*, 2011). Latitudinal, altitudinal and regional clines along environmental gradients have been observed for adaptive traits and genetic markers related to thermal tolerance (Watt, 1983; Rank & Dahloff, 2002; Hoffmann, Shirriffs & Scott, 2005; Kyriacou *et al.*, 2008; Collinge *et al.*, 2008; Fry, Donlon & Saweikis, 2008; Karl, Schmitt & Fisher, 2009; Paaby *et al.*, 2010), phenological traits (Masaki, 1999; Stinchcombe *et al.*, 2004; Schmidt *et al.*, 2008*b*), dispersal capacity (Haag *et al.*, 2005; Saastamoinen & Hanski, 2008) and life-history traits (Schmidt & Paaby, 2008; Klemme & Hanski, 2009; Paaby *et al.*, 2010; Montesinos-Navarro *et al.*, 2011). The study of geographic clines in multiple genetic markers allows the identification of candidate genes implied in the regulation of adaptive traits that interact with environmental gradients and probably contribute to determine the distribution of species along them (Schmidt *et al.*, 2008*a*; Blackman, 2010; Paaby *et al.*, 2010). Interestingly, these studies of adaptive clinal variation can be performed at multiple spatial scales, ranging from local-scale gradients to latitudinal clines (e.g. Schmidt *et al.*, 2008*a*). Moreover, they allow the discrimination of neutral from adaptive genetic variation (Schmidt *et al.*, 2008*a*, Michel *et al.*, 2010).

The burst of genomics and transcriptomics now allows the study of the clinal variation of genome structure along geographic gradients, including the study of clinal variation in available annotated genes, transposable elements, inversions and speciation genes (Hohenlohe *et al.*, 2010; González *et al.*, 2010; Kolaczkowski *et al.*, 2011, Wolf, Lindell & Backström, 2010; Nosil & Schluter, 2011; Rice *et al.*, 2011). Genomic studies suggest the existence of pervasive spatially varying selection acting at key genes throughout multiple genetic and metabolic pathways (Kolaczkowski *et al.*, 2011; Hohenlohe *et al.*, 2010). For instance, genomic studies in latitudinal clines of *Drosophila melanogaster* have revealed the existence of pervasive adaptive variation in a wide number of genes coding for several key biological processes like cis-acting gene regulatory processes, transcription, chromatin regulation, circadian biology, development and body size growth (Kolaczkowski *et al.*, 2011). Other studies suggest that this adaptive variation in fitness-associated loci has important effects on whole genome structure through diverse related processes (Nosil, Funk & Ortiz-Barrientos, 2009; Michel *et al.*, 2010). For instance, divergent selection also strongly influences the evolution of tightly and loosely linked neutral loci via linkage effects (gene hitchhiking). It also interacts with chromosomal inversion processes in diverse complex ways and facilitates genetic divergence. Finally, divergent selection can reduce gene flow and gene introgression from nearby populations, due to reduced fitness of immigrant genotypes, and therefore promotes genetic drift in neutral regions of the genome (Nosil, Funk & Ortiz-Barrientos, 2009; Michel *et al.*, 2010).

(5) Multivariate adaptive trait continuums

It has been shown recently that diverse adaptive traits and their interactions with the local environment influence the distribution of species along species richness gradients (e.g. Thuiller *et al.*, 2004; Stefanescu *et al.*, 2011*a*). Interestingly, some adaptive traits can be measured across many species allowing comparative approaches at the inter-specific level. These analyses have revealed the existence of suites of traits that tend to co-vary along a main axis of variation at the inter-specific level in plants (Grime *et al.*, 1997; Wright *et al.*, 2004; Chave *et al.*, 2009; Donovan *et al.*, 2011), mammals (Bielby *et al.*, 2007 and citations therein), birds (Sæther *et al.*, 2011), fishes (Jeschke & Kokko, 2009), phytoplankton (Litchman & Klausmeier, 2008), marine bacteria (Lauro *et al.*, 2009) and butterflies (Fig. 3). Adaptive trait continuums can be described easily and quantified using principal components analysis (PCA) or other ordination techniques (e.g. Wright *et al.*, 2004; Lauro *et al.*, 2009; Fig. 3). These continuums often range from specialized to more generalist species and/or from slow to fast lifestyles (Wright *et al.*, 2004; Bielby *et al.*, 2007; Sæther *et al.*, 2011; Fig. 3). The mechanistic origin of these taxon-specific trait continuums relies on the evolutionary emergence of contrasting life-history strategies that, in particular ecological contexts, maximize fitness by acquiring a different set of traits allowing for sustained population performance. Overall, adaptive trait continuums describe main axes of trait co-variation at the inter-specific level and quantify life-history variation and "phenotypic space" (*sensu* Donovan *et al.*, 2011).

Here we suggest that adaptive trait continuums may provide a useful mechanistic framework linking demography, gene flow and diversification dynamics along species richness gradients. For instance, an adaptive trait continuum is observed among 169 Mediterranean butterflies distributed along a regional species-richness gradient in Catalonia, Spain (Fig. 3; Stefanescu *et al.*, 2011*a*,*b*). For each species, we measured habitat thermal breadth, habitat aridity tolerance, dispersal capacity, host-plant diet breadth, and phenology (number of months with flight activity) (data from Stefanescu *et al.*, 2011*a*; see online supporting information, Appendix S1 for further details). A main inter-specific axis of variation across these traits accounted for 60% of the variation, ranging from specialist to generalist butterflies. The adaptive trait continuum (PCA scores) correlated with long-term demographic trends observed in the region (showing significantly higher declines in specialists, Fig. 3B) and, more generally, with observed differences in spatial genetic structure (F_{ST}, Fig. 3A). PCA scores of the adaptive trait continuum also co-varied with the distributional ranges of the species along the gradient (Fig. 3C), as illustrated for monophagous, oligophagous and polyphagous butterflies (Fig. 3D).

(6) Community context, adaptive behavioural traits, morphological divergence and speciation

Community context, i.e. the geographical variation in community composition and species interactions, can

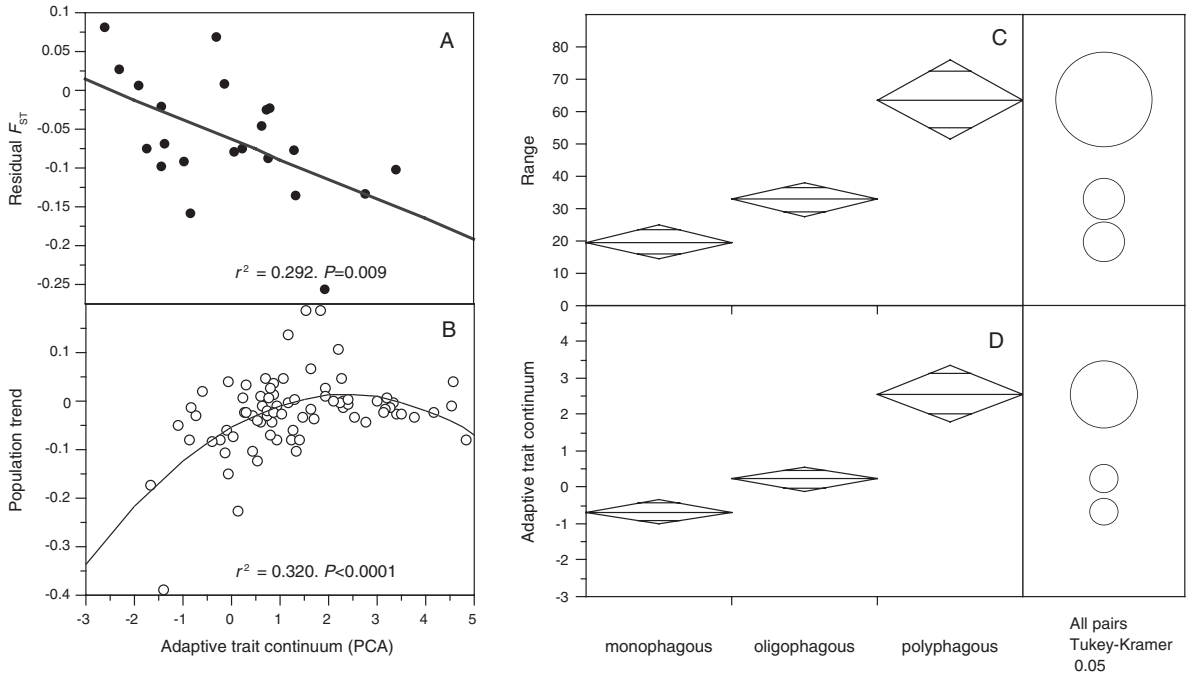

Fig. 3. An example of the observed relationships between an adaptive trait continuum and (A) F_{ST} values reported for European butterflies (Nève, 2009), (B) long-term butterfly population trends in Catalonia (Stefanescu *et al.*, 2011*a*), and (C, D) species' distributional ranges in Catalonia, Spain. A principal components analysis (PCA) was performed between dispersal capacity, number of host-plant species used, phenology (number of weeks with flying activity per year), habitat temperature breadth and habitat aridity tolerance breadth for 169 butterfly species [data sources from Stefanescu *et al.* (2011*a*) and unpublished phenological data]. A main axis accounted for 60% of the variation in these traits and habitat variables (PCA variable). This PCA variable ranges from specialist lifestyles (monophagous with short phenology) to generalist lifestyles (polyphagous with wide phenology). The adaptive trait continuum correlates with the estimates of F_{ST} for European butterflies (values corrected for the spatial scale of each study extracting regression residuals between the spatial distance of the study and the reported F_{ST} values), the long-term population trends in Catalonia and the butterfly species ranges in Catalonia (number of transect routes on which the species was detected, see online supporting information, Appendix S1 for further details). Monophagous butterflies feed on plants of a single genus, oligophagous on plants of various genera from the same family, and polyphagous species on a diversity of plants belonging to various families. In C and D the line across the centre of each diamond represents the group mean. The vertical span of each diamond represents the 95% confidence interval for each group. Short horizontal lines near the top and bottom of each diamond are overlap marks at $(\frac{\sqrt{2}}{2}) * CI$ above and below the group mean. Each pair of group means may be compared visually by examining how the comparison circles intersect. Circles for means that are significantly different do not intersect (Tukey-Kramer test, $P < 0.0001$). Additional information is provided as online supporting information, Appendix S1.

influence the outcome of speciation and adaptive trait diversification processes (McPeek, 1996; Thompson, 2005; Abrams, 2006; Johnson & Stinchcombe, 2007; Carnicer, Abrams & Jordano, 2008*a*; Elias *et al.*, 2008; Schemske *et al.*, 2009). Therefore, a necessary step in order to understand fully the generation of species richness gradients is to elucidate which specific community contexts allowed increased diversification rates in each particular area and taxon. Empirical studies indicate that spatial and temporal variation in community context effectively cause geographical mosaics of selection, leading to morphological divergence and, in some cases, to speciation (Thompson, 2005). For instance, geographical differences in local community composition, such as the presence or absence of resource competitors, have been found to promote the emergence of morphologically distinct populations in crossbills (Benkman, Holimon & Smith, 2001; Parchman & Benkman, 2002; Benkman, 2003). These studies show that direct interactions among two community species (e.g. lodgepole pines and squirrels) can indirectly alter the nature of selection experienced by birds, and thus highlight the importance of community context in explaining diversification processes in adaptive morphological traits. Similarly, in butterflies, mutualistic interactions like Müllerian mimicry have been found to drive local adaptive trait variation with potential implications in diversification processes (Elias *et al.*, 2008).

Another aspect of community context that can facilitate morphological diversification is the uneven spatial and temporal distribution of resources (Price, 2008). For instance, fruits are predominantly confined to upper vegetation layers (Levey, 1988; Loiselle, 1988; Loiselle & Blake, 1991; Moles & Westoby, 2003; Moles *et al.*, 2004; Schleuning *et al.*, 2011) and invertebrate types and abundances differ strongly among adjacent vegetation types (Johnson *et al.*, 2005; Blondel *et al.*,

2006). Similarly, seasonality in resource variation is higher at upper vegetation layers but is usually less marked at the ground and understorey levels (Blondel, 1969; Poulin & Lefebvre, 1996). Empirical and theoretical evidence suggests that this uneven distribution of resources might promote ecological speciation through the evolutionary emergence of different feeding behavioural strategies with contrasting adaptive morphological traits (Feinsinger & Swarm, 1982; Smith *et al.*, 1997; Abrams, 2006; Carnicer *et al.*, 2008*a*; Carnicer, Jordano & Melián, 2009).

Finally, different community contexts can also induce changes directly on morphology through behavioural plastic responses (Agrawal, 2001; Price, Qvarnström & Irwin, 2003; Sol & Price, 2008). For example, some behavioural responses, such as resource switching behaviour, have been found to be pervasive and widespread in some bird communities (Fig. 4). Notably, different behavioural responses induced by community context are associated with morphological differences between bird species in adaptive traits (Fig. 4), providing some support for a role of community context and behavioural plasticity in bird morphological diversification and speciation processes (see Price *et al.*, 2003; Abrams, 2006; Sol & Price, 2008; Carnicer *et al.*, 2008*a*).

IV. EMERGING RESEARCH LINES AND TRENDS

In this section we briefly summarize a diverse suite of trait-based approaches in evolutionary ecology. These approaches may provide new tools and guidelines for future studies of species richness gradients.

(1) Genomics and transcriptomics may provide new ways to the study of the clinal variation of trade-offs between traits across gradients (Bochdanovits & de Jong, 2004; St-Cyr, Derome & Bernatchez, 2008), and may facilitate the study of genomic reaction norms and phenotypic plasticity across gradients (Gracey *et al.*, 2004; Aubin-Horth & Renn, 2009; Pfennig *et al.*, 2010). In addition, genome-scale models now enable the computation of phenotypic traits based on the genetic composition of the target organism (reviewed in Palsson, 2009).

(2) The emerging field of comparative phylogenomics allows the analysis of the evolution of networks of regulatory genes related to specific adaptive traits (e.g. chemosensory systems determining host-plant choice and specialization in insects) (Tsong, Tuch & Johnson, 2006; Prud'homme, Gompel & Carrol, 2007; McBride & Arguello, 2007; Singh *et al.*, 2009; Pigliucci, 2010; Vieira & Rozas, 2011, Álvarez-Ponce, Aguadé & Rozas, 2011), and the analysis of the rise, spread, and death of gene families across phylogenies (Demuth & Hahn, 2009; Vieira & Rozas, 2011). All these approaches could be applied to the study of adaptive traits that influence speciation dynamics and the distribution of species across environmental gradients (e.g. Seehausen *et al.*, 2008; Kellermann *et al.*, 2009).

(3) The application of a diverse set of phylogenetic methods facilitates the study of the ecological and evolutionary mechanisms implied in the genesis and maintenance of species richness gradients. For instance, new phylogenetic procedures are available to estimate trait-dependent speciation and extinction rates from incompletely resolved phylogenies (Fitzjohn, Maddison & Otto, 2009), perform hierarchic analyses of species richness gradients (Heard & Cox, 2007), assess time-for-speciation effects (Smith *et al.*, 2007; Kozak & Wiens, 2010; Wiens *et al.*, 2011); discern the effect of local competition and niche conservatism effects (Lovette & Hochachka, 2006), model trait evolution along phylogenies (Ree *et al.*, 2005; Ree, 2005; Paradis, 2005; Van Bocxlaer *et al.*, 2011), describe hybrid zones and phylogeographic breaks (Hewitt, 2001; Saetre *et al.*, 2001; Swenson & Howard, 2005), explore the relative roles of speciation and extinction rates in shaping diversification rates (Lovette, 2005; Weir, 2006; Weir & Schluter, 2007; Rabosky, 2010), test whether speciation is slowing down over time (Zink & Slowinski, 1995; Pybus & Harvey, 2000; Johnson & Cicero, 2004; Weir, 2006; Rabosky, 2009), assess differences in rates of diversification among clades (Barraclough & Nee, 2001; Cavender-Bares & Wilczek, 2003; Phillimore *et al.*, 2007; Wiens, 2007), assess differences in the rates of evolution of different traits or genes (Ackerly, 2009; Singh *et al.*, 2009), explore the role of trait evolution and assembly rules in structuring communities (Cavender-Bares & Wilczek, 2003; Ackerly *et al.*, 2006; Silvertown *et al.*, 2006; Lovette & Hochachka, 2006; Kraft *et al.*, 2007), analyze modes of geographical speciation (Barraclough & Vogler, 2000; Coyne & Price, 2000; Crisp *et al.*, 2009; Pigot *et al.*, 2010; Goldberg, Lancaster & Ree, 2011), quantify temporal variation in immigration and extinction rates in archipelagos (Ricklefs & Bermingham, 2001, 2004) and assess latitudinal divergences in diversification rates (Cardillo, 1999; Cardillo, Orme & Owens, 2005; Barraclough & Nee, 2001; Weir, 2006; Weir & Schluter, 2007; Rabosky, 2010; Kozak & Wiens, 2011).

(4) The identification of the genetic and developmental paths that control morphological traits and adaptive behaviours ["behavioural genes" *sensu* Fitzpatrick *et al.*, (2005)] provides a new tool to study diversification processes. For example, some pioneering works have identified some genes and developmental paths of traits putatively implied in bird speciation processes. These genes and metabolic paths are possibly shared by most bird species and might become a powerful tool for the comparative study of morphological diversification (Wu *et al.*, 2004; Abzhanov *et al.*, 2004, 2006; Fitzpatrick *et al.*, 2005, Campàs *et al.*, 2010; Mallarino *et al.*, 2011).

(5) Studying dispersal and movement behaviour along species richness gradients is likely to become more feasible with advances in molecular techniques and tracking technology and the application of recently developed theoretical frameworks (Bowler & Benton, 2005; Holyoak *et al.*, 2008; Nathan *et al.*, 2008; Revilla & Wiegand, 2008; Clobert *et al.*, 2009; Hanski & Mononen, 2011; Wheat *et al.*, 2011). Future studies should highlight how individual movements and spatial population dynamics influence altitudinal and latitudinal species richness gradients.

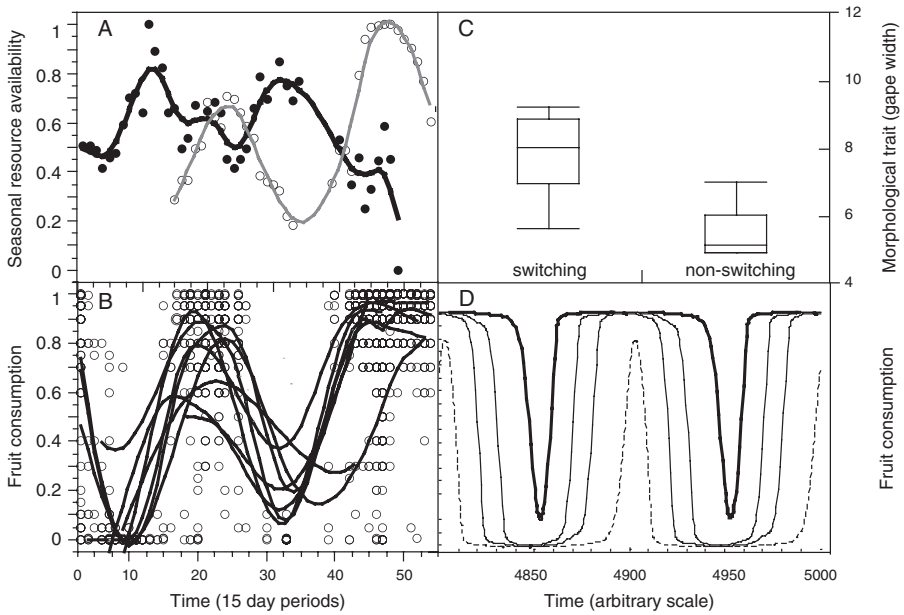

Fig. 4. An example of the possible role of adaptive switching behaviour in promoting morphological diversification of foraging traits. Bird communities are often characterized by seasonal variation in resource supply. Birds respond to seasonal resource fluctuations with behaviourally plastic responses. Here we show an example of a Mediterranean bird community located in South-western Spain. (A) Black dots illustrate the seasonal variation in insect abundance in a Mediterranean shrubland over two years. White dots represent the seasonal variation in fruit abundance. The resources present alternate peaks, with spring peaks of insects and fruits peaking in autumn. (B) Observed behavioural responses of the birds switching in response to seasonal variation in resource supply. Each line represents a different species. Each dot represents a fecal sample in which the percentage of fruits and insects in the diet was measured. The bulk of these species switch between resources matching the seasonal fluctuations in resource supply. Species differ in the speed of switching responses, presenting rapid and delayed switching responses to resource fluctuation. Some species behave as specialists in one of the two resource channels. Delayed switchers and specialists are not shown. (C) Differences in behaviour are associated with morphological differences in foraging traits. Switching species have wider gapes than specialists. The line across the middle of the box identifies the median sample value. The ends of the box are the 25th and 75th quantiles. (D) Recent theoretical models (Abrams, 2006) demonstrate that behavioural switching between two food types in a variable environment promotes coexistence and evolutionary diversification of foraging adaptive traits of competing species. Diversification is caused by disruptive selection of a morphological foraging trait that is related to the relative use of two food types or resource channels. The figure illustrates the theoretical expected switching behavioural dynamics of the evolutionarily stable coalition for four generalist species derived from the Abrams (2006) model. Full details of the simulation are provided as online supporting information (Appendix S2); see Abrams (2006) and Carnicer *et al.* (2008*a*) for an explanation and analysis of the model.

(6) The empirical study of behavioural dynamics on target species along environmental gradients (e.g. Snell-Rood & Badyaev, 2008) should be accompanied by the empirical estimation of demographic parameters (dispersal, survival, fecundity, population variability) (Zang, 1980; Badyaev & Ghalambor, 2001; Sæther *et al.*, 2008, 2011) and habitat quality measures (*sensu* Jonhson, 2007). Community-wide evaluations of plastic behavioural responses (e.g. Carnicer *et al.*, 2008*a*, 2009) are required to evaluate the role of behaviour on diversification dynamics and to assess the geographical variation of adaptive behaviours along environmental gradients (Jetz & Rubenstein, 2011).

(7) The seasonal distribution of resource availability has been identified as a major cause of the evolutionary origin of migration (Salewski & Bruderer, 2007; Boyle, 2008), a behavioural adaptive trait that strongly influences the shape and temporal variation of species richness gradients (Hurlbert & Haskell, 2003; Carnicer & Díaz-Delgado, 2008). More detailed and extensive empirical studies addressing the spatial and seasonal variation of resources along species richness gradients are needed (Hurlbert & Haskell, 2003; Buler, Moore & Woltmann, 2007; Peters *et al.* 2010). Seasonal patterns of resource variation are linked to migration movements, life-history evolution and may also drive diversification dynamics at longer temporal scales (Johnson *et al.*, 2005; Novotny *et al.*, 2007; Buler *et al.*, 2007; Boyle & Conway, 2007; Price, 2008; Carnicer *et al.*, 2008*a*, 2009; Boyle, 2008). Some pioneering studies are starting to describe global patterns in resource seasonality (Ting *et al.*, 2008). Interestingly enough, global patterns in seasonality of fruit resources are correlated with measures of actual evapotranspiration (Ting *et al.*, 2008), and other global predictors of species richness gradients like temperature (Hawkins *et al.*, 2003*a*, *b*).

(8) An increasing number of theoretical models also provide insights into the evolutionary and ecological processes

that mould species richness gradients (Tables 2, 3), like diversification dynamics (Dieckmann & Doebeli, 1999; Hubbell, 2001; Case & Taper, 2000; Doebeli & Dieckmann, 2003; Gavrilets & Vose, 2005; Abrams, 2006; Roy & Goldberg, 2007; Rangel, Diniz-Filho & Colwell, 2007; Bolnick & Fitzpatrick, 2007; Arita & Vázquez-Dominguez, 2008; Carnicer *et al.*, 2008*a*; van Doorn, Edelaar & Weissing, 2009; Heinz *et al.*, 2009; Gavrilets & Losos, 2009; Faria & Navarro, 2010; Rosindell & Phillimore, 2011) and other complementary processes like dispersal limitation, niche filtering and demographic stochasticity (Hubbell, 2001; Rangel & Diniz-Filho, 2005; Rangel *et al.*, 2007; Hugueny, Cornell & Harrison, 2007; Kadmon & Allouche, 2007, Rosindell & Phillimore, 2011), habitat selection (Fretwell & Lucas, 1970; Morris, 2003; Fletcher, 2006) or gene-flow in metacommunities (Urban & Skelly, 2006, Urban *et al.*, 2008).

V. CONCLUSIONS

(1) Species characterized by more specialized adaptive traits show spatially nested distributions along species richness gradients (Fig. 2) (Carnicer *et al.*, 2008*a*; Stefanescu *et al.*, 2011*a*; Alexander *et al.*, 2011). Rare species also show higher effects of demographic stochasticity, asynchronous and more isolated population dynamics, low dispersal fluxes and greater spatial genetic variation. By contrast, widespread generalists often show more synchronous spatial population dynamics, demographically track environmental variation and resource peaks, experience lower effects of demographic stochasticity, attain higher population sizes, and are characterized by lower spatial genetic variation (Sæther *et al.*, 2011; Fig. 3). Demographic dynamics differ greatly between species located at opposite extremes of adaptive trait continuums (Sæther *et al.*, 2011; Shultz *et al.*, 2005; Fig. 3). Adaptive trait continuums usually range from fast to slow and/or from specialist to generalist lifestyles.

(2) More empirical studies quantifying the effects of environmental conditions on the deterministic and stochastic components of population dynamics along latitudinal and altitudinal species richness gradients are required (e.g. Sæther *et al.*, 2003, 2008, 2011). These studies should provide a better description of the geographic mosaics in population dynamics that are associated with the maintenance of species richness gradients (Table 2).

(3) A related issue is the study of the geography of colonization and extinction rates along species richness gradients. Recent studies have found geographic differences in extinction rates along regional species richness gradients (e.g. Carnicer *et al.*, 2007, 2008*b*; Fig. 2). Greater extinction rates in specialists are frequently observed (Kotiaho *et al.*, 2005; Shultz *et al.*, 2005). However, more studies are required to achieve a precise knowledge of which adaptive traits and behaviours are moulding demographic and dispersal rates (e.g. Sæther *et al.*, 2003, 2008, 2011; Brotons, Pons & Herrando, 2005; Sirami, Brotons & Martin, 2008).

(4) Empirical evidence suggests that adaptive traits associated with thermal tolerance, resource use, phenology and dispersal capacity play a significant role on setting the limits of species' distributions along altitudinal and latitudinal gradients. Complementary studies also assert that other life-history traits (e.g. lifespan, fecundity, survival, body size) frequently interact with phenology, dispersal and thermal-tolerance traits across latitudinal and regional clines (Schmidt & Paaby, 2008; Klemme & Hanski, 2009; Paaby *et al.*, 2010; Kolaczkowski *et al.*, 2011). Future studies dealing with species richness gradients should explicitly consider phenological and behavioural schedules (e.g. insect voltinism and diapause cycles; plant and animal annual cycles) and plastic adaptive behaviours (e.g. behavioural barriers to dispersal, condition-dependent dispersal).

(5) Several studies highlight that functional groups characterized by different suites of adaptive traits are differentially distributed across species richness gradients (Carnicer & Díaz-Delgado, 2008; Stefanescu *et al.*, 2011*a*; Kissling, Sekercioglu & Jetz, 2011; Lennon *et al.*, 2011, Ekross & Kuussaari, 2011; Alexander *et al.*, 2011). Therefore, the identification and separate study of functional groups facilitates the ecological interpretation of species richness gradients (Carnicer & Díaz-Delgado, 2008; Kissling, Böhning-Gaese & Jetz, 2009). Similarly, quantifying and mapping trait variation across geographic gradients warrants further scientific effort (Reich, Walters & Ellsworth, 1997; De Jong & Bochdanovits, 2003; Reich & Oleksyn, 2004; Sørensen *et al.*, 2005; Kyriacou *et al.*, 2008; Jetz, Sekercioglu & Böhning-Gaese, 2008; Jetz & Rubenstein, 2011).

(6) Adaptive trait continuums may provide a powerful mechanistic framework to: (1) analyze life-history variation across species-richness gradients, (2) explore correlates with demography and gene flow estimates, and (3) to explain inter-specific differences in long-term diversification trends. Improved descriptions of inter-specific trait continuums may be achieved by integrating data at several hierarchical levels (genome, transcriptome, proteome, metabolome, interactome, regulome, fluxome, phenome, environmental and demographic data) using available high-throughput technologies (e.g. Lauro *et al.*, 2009; Macel, Van Dam & Keurentjes, 2010; Houle, Govindaraju & Omholt, 2010; Raes *et al.*, 2011).

(7) Mechanistic approaches linking genotype, phenotype, organism performance and fitness are becoming available for some adaptive traits that limit species distributions (Dalziel *et al.*, 2009; Dillon *et al.*, 2009; Storz & Wheat, 2010). These mechanistic approaches are also becoming available for traits involved in reproductive isolation and speciation processes along gradients (Seehausen *et al.*, 2008; Rice *et al.*, 2011). Generally, the analysis of integrated mechanistic approaches is currently facilitated by the parallel burst of genomics, transcriptomics, metabolomics, metagenomics and phenomics (Palsson, 2009; Macel *et al.*, 2010; Houle *et al.*, 2010). Indeed, new studies are using 'omic' techniques to study clinal variation of adaptive traits and genetic markers across latitudinal, altitudinal and regional environmental gradients (Michel

et al., 2010; González *et al.*, 2010; Kolaczkowski *et al.*, 2011; Raes *et al.*, 2011; Gianoulis *et al.*, 2009; see Section IV). These studies report pervasive adaptive clinal variation related to a great variety of biological processes and molecular markers (Michel *et al.*, 2010; Hohenlohe *et al.*, 2010; Kolaczkowski *et al.*, 2011).

(8) Several researchers have pointed out that the explicit consideration of adaptive traits and plastic behaviours can profoundly change the behaviour of theoretical models (e.g. Reed & Levine, 2005; Fletcher, 2006; Abrams, 2006). For instance, recent theoretical works (Kondoh, 2003; Abrams, 2006; Rueffler, Van Dooren & Metz, 2007; van Doorn *et al.*, 2009; Pfennig *et al.*, 2010; Snell-Rood *et al.*, 2010; Moczek *et al.*, 2011) highlight the importance of adaptive behaviours and phenotypic plasticity on diversification and population interaction dynamics. Models of clinal speciation explicitly simulate the evolution of traits and diversification processes across environmental gradients (Doebeli & Dieckmann, 2003; Heinz *et al.*, 2009). Similarly, fitness-based models that explicitly incorporate adaptive traits and phenology have been successfully applied to predict species' distributions (Kearney & Porter, 2009; Chuine, 2010).

(9) Clade-specific studies of the sequential evolution of adaptive traits along phylogenies and their relationship with diversification rates are improving our current understanding of adaptive radiations, diversification processes and the history of clade migrations (Böhning-Gaese *et al.*, 2003; Davies *et al.*, 2004; Freckleton & Harvey, 2006; Wiens, 2007; Menken *et al.*, 2009; Hodges & Derieg, 2009; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010; Section IV).

(10) To assess effectively the importance of community context in driving diversification processes new research should be conducted in several areas: (1) the study of the spatial and temporal variation of community context (i.e. consumer-resource interaction networks) along geographical gradients of species richness (Callaway *et al.*, 2002; Olesen & Jordano, 2002; Schemske *et al.*, 2009; Carnicer *et al.*, 2009; Moya-Laraño, 2010; McKinnon *et al.*, 2010, Rasmann & Agrawal, 2011), (2) the quantitative study of the spatial and temporal variation of resource distribution along species richness gradients (Johnson *et al.*, 2005; Novotny *et al.*, 2007; Ting, Hartley & Burns, 2008), and (3) the comparative examination of phenotypically plastic responses along species richness gradients (Smith *et al.*, 1997; Price *et al.*, 2003; Sol & Price, 2008; Abrams, 2006; Carnicer *et al.*, 2008*a*; Aubin-Horth & Renn, 2009; Pfennig *et al.*, 2010; Snell-Rood *et al.*, 2010; Moczek *et al.*, 2011).

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Supplementary methods and information for Fig. 3.

Appendix S2. Supplementary methods and information for Fig. 4.

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